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Mechanisms in Fungal Succession

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INTRODUCTION

"Community life for a fungus is dynamic" (Frankland, 1981). This statement is as true a decade later as when made, although now it could well be updated to include events within populations, emphasizing our greater appreciation of interactions between individual mycelia of single species. Fungal successions, the changing spatial and temporal patterns in communities and populations, even if not fully understood are familiar to all mycologists. Each one is unique, the outcome of the interplay of a bewildering number of different circumstances, but some general patterns and processes can be discerned. These are discussed in this chapter with special reference to terrestrial, non-pathogenic fungi of soil, roots and plant litter.

THE NATURE OF SUCCESSIONS

In the study of succession, higher plant ecologists have led the way, developing a highly quantitative and predictive science from much early theorizing. At the beginning of the century botanists tended to be preoccupied with theory, and Clements, author of the classic *Plant Succession. An Analysis of the Development of Vegetation* (1916), went too far in attempting to equate a plant community with an organism that could grow, mature and die. Nevertheless, he was largely responsible for introducing the dynamic principle into ecology (Miles, 1979). Mycologists followed behind, adopting the new attitude but slow to take account of the differences between higher plants and fungi, or to divorce themselves from inappropriate concepts. Now the emphasis is on processes, and ecologists are abandoning the search for unifying theories of succession (Miles, 1987).

Some Terminology

Succession when defined as 'a directional change in the composition, relative abundance, and spatial pattern of species comprising communities' can be applied to both vegetation and fungi. In mycological terms, it is more precisely 'the sequential occupa-

tion of the same site by thalli (normally mycelia) either of different fungi, or of different associations of fungi' (Rayner and Todd, 1979). Possession of an indeterminate form of growth, unlike that of a static, circumscribed plant, obviously has far-reaching consequences.

The most fundamental difference between successions of saprotrophic fungi and those of higher plants lies in the build-up in the latter to a so-called 'climax' community (if the environment is relatively stable), and the reduction in the former to a theoretical zero when the resource is exhausted. In practice, fungal successions on decomposing organic matter are rarely followed to this end-point, and investigations of the fungal decay of the refractory remains of plants within soil have been limited.

Further differences between decomposer and so-called ecosystem successions have been hypothesized by Swift (1976, 1982a), but they require verification. In general, it can be said that an increase in the diversity of fungal species is accompanied by an increase in nutrient release from the system, in contrast to the pattern of events in plant succession even if the latter is not consistent in direction (Peet and Christensen, 1980). A succession of mycorrhizal fungi on a host root is perhaps more akin to that of vegetation since the resource in the short-term is renewable, but pursuit of such comparisons is not particularly rewarding.

Classification of fungal successions can help to clarify their nature, although the extreme versatility of fungi precludes rigid demarcations. Park's (1968) division of fungal successions into the substratum and seral type has been widely adopted, but these terms should not be accepted without some reservations. A 'substratum' is strictly just the medium that physically supports a fungus, whereas it is now common practice to denote the material that sustains fungal growth as the 'resource' (Swift, 1976; Rayner et al., 1985). Theoretically, therefore, 'resource succession' would perhaps be a more appropriate term for the succession of species that occurs on any colonizable plant, animal or man-made material. In practice, however, the resource is often less discrete and recognizable than the substratum. A cellulose film buried in soil, as described in classic studies of succession by Tribe (1957, 1961), is a single resource, but a leaf or fallen tree trunk is a heterogeneous complex of closely interrelated resources, usually exhibiting a pattern of decomposers related to the distribution of different tissues. Swift (1976, 1984) attempted to overcome this problem by terming the latter a 'unit resource' supporting a 'unit community'. The ability of fungi to obtain nutrients from sources well beyond the limits of their substrata is a further complication.

Seral successions of fungi have rarely been described. Typically they are associated with the vegetation seres of a developing ecosystem, such as a forest continuum or sand dune system, in which the supply of resources changes progressively. Changes in the green plant community regulate the decomposer community. Reactions between the two are reciprocal, but the accumulation of organic matter tends to 'drag' the decomposer succession in the wake of the higher-plant succession (McNaughton and Wolf, 1973). In effect, each seral succession of fungi is a bird's eye view of a series of interrelated substratum successions.

Grubb (1987) objected to Park's terminology on semantic grounds, preferring to describe fungal successions as substratum-level or community-level. The first is surely a quibble, proliferating terms unnecessarily, and the second could lead to confusion between higher-plant and fungal communities. The term 'community' in itself is beset with problems of definition. If a fungal community is 'an assemblage of diverse species occupying the same, functionally discrete, environment or ecosystem' (Cooke and Rayner, 1984), the mycoflora of both a leaf and a sand dune could qualify, although nei-

ther is likely to be truly self-contained. A community of fungi like those of higher plants is a concept of convenience rather than a crisply defined entity (Levin, 1989). 'Seral' is not ideal in its connotation, but it emphasizes more closely the interplay between successions at more than one ecosystem level.

Fungal successions are also classified as primary or secondary, but the division is again somewhat arbitrary. A typical primary succession originates on a virgin surface or site—a pioneer situation. In contrast, a secondary succession follows disruption of a primary succession by a sudden event that gives access to new resources, and propagules of the first colonizers are typically present at the outset. An excellent example of this, resulting from frequent fires in the chaparral shrublands of California, has been described in detail by Wicklow (1988, and earlier papers). Reduction of competition and soil toxicity by fire enabled both ascospores and seeds already present on the burnt sites to germinate and colonize.

Many examples of alternatives to the main pathways of succession could be quoted. Events such as fire are destructive, but others such as leaf fall 'disturb' community development by enrichment (Pugh and Boddy, 1988). Cycles, and fluctuations that vary about a notional mean, are also frequent within a forwardly-directed succession, driven in particular by changes in life-form and season. Again, latent invaders, activated by changes in the micro-environment, are a feature of the colonization of wood in particular (Rayner and Boddy, 1988a). A system may even be 2-tiered if mycelium itself is colonized by another species without replacement. The terminology of succession must, therefore, accommodate a multidimensional phenomenon not a simple linear process.

Substratum Succession

Numerous substratum successions of saprotrophic fungi have been described, most on plant material above the soil (Dickinson and Pugh, 1974), and their general characteristics have been compared by Hudson (1968), Frankland (1981), Swift (1982a), and Cooke and Rayner (1984). A succession that has been observed on decomposing petioles of the fronds of bracken (*Pteridium aquilinum* L. Kuhn) is briefly outlined here as an example (Frankland, 1966, 1969, 1976; Fig. 1).

The standing but senescent fern was colonized in late summer by weak pathogens, such as the host-restricted, lesion-forming *Rhopoglyphus filicinus*, and hyphae had penetrated the non-lignified cortex and phloem. The cosmopolitan *Aureobasidium* had also formed superficial lesions, which followed the long axis of the plant cells along possible lines of weakness or channels of water and nutrients, and remained for a year after frond fall. By the end of the first year, generalized breakdown of the epidermis and outer cortex by the primary saprotrophs had occurred and the phloem was no longer recognizable. At the same time, Basidiomycotina were attacking the lignified cells walls, becoming most prominent in the second-year litter. This resulted in removal of 50% of the holocellulose by the third year and 50% of the lignin by the fourth year. Overlapping waves of secondary saprotrophs, including mucoraceous and predaceous species and increasingly typical of a soil mycoflora, followed. Many of these later colonizers entered xylem elements and fibers through disrupted pits. By the end of the fifth to sixth year, depending on soil type, the C:N ratio had decreased from approximately 200 to 30, and the pH had increased from 5 to 6. At this stage fungal activity was virtually at a standstill and bacteria had replaced hyphae in the most rotten samples.

Soil invertebrates were active from the third year after frond fall onwards. Large numbers of foraging Collembola and Acarina, often coated with fungal spores, were

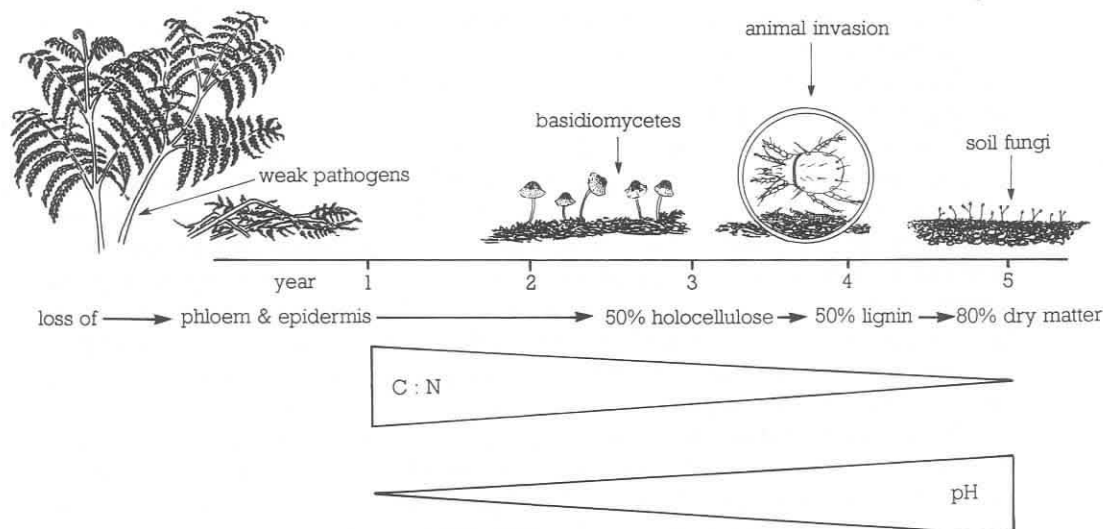


Figure 1 Successional stages in the decomposition of petioles of *Pteridium aquilinum*.

seen inside the petioles pushing the softer tissues aside and grazing heavily but selectively on fungal tissue, and, therefore, influencing the course of succession. This type of animal involvement in fungal succession has been discussed in detail by Visser (1985) and Shaw (this volume).

The wave pattern of succession on bracken petioles is typical of that described on many other herbaceous litters, although it is sometimes more imaginary than real, many species being present at the outset but dominating at different points in time. The sequence here in which lignin decomposers precede most of the mucoraceous fungi is really more characteristic of woody substrata than herbaceous material (see Rayner and Boddy, 1988a). It can be hypothesized that this is related to the delayed release of simple carbohydrates in bulky, lignified materials, but it has not been verified in the field.

Seral Succession

Seral successions of fungi can be illustrated by the soil mycoflora associated with changes in vegetation across some developing dune systems (Brown, 1958a; Frankland, 1981). Gradient series of fungal communities, stretching from the seashore and mobile foredunes to the semi-fixed dunes and then to grassland, heath or woodland on old fixed dunes, were examined in eight acid and alkaline, coastal systems of the British Isles. The classic seral successions of dune vegetation were found to be mirrored by changes in the sand mycoflora, so that the center of each of six or more seres could be recognized as readily by the assemblage of fungi isolated on a culture plate, inoculated with only 5 mg of sand, as by the community of higher plants. The technique selectively isolated species as spores or hyphal fragments from a whole spectrum of substrata, including sand grains coated by a nutrient film and even rotting bracken petioles(!). The plate mycoflora although distinctive was, therefore, in essence a laboratory artefact. It indicated the presence and possibly the abundance of certain species in a sere but gave no hint of the nature of their resources or state of activity. Several features, however, emphasized how closely the two ecosystem levels—autotrophic and heterotrophic—were integrated.

For example, the greatest diversity of fungal species occurred at an intermediate stage, in samples from 100-year-old, semi-fixed dunes where pioneer and late successional plants overlapped, a pattern often described in higher-plant successions (Horn, 1974). Overall, the mycoflora became less variable as conditions stabilized, but, with increasing stratification of the vegetation and development of a soil profile, distinct fungal 'horizons' of different species composition were formed. Fungal productivity was not recorded, but biomass (abundance of mycelium) reached a maximum in 240-year-old fixed dunes (Brown, 1958b). Despite this appearance of a certain equilibrium in the final stages of the succession, it cannot be equated in any way with a Clementsian climax.

The occurrence of *Ammophila arenaria* (L.) Link in every zone of these dune systems, both acid and alkaline, provided an unusual opportunity for examining a specific, even if not identical, substratum throughout a seral succession. Root sampling showed that the association between the root surface of this grass and saprotrophic fungi was not a highly selective one (Frankland, 1981). The root community changed progressively with ecosystem development, and became less and less distinct from that of the open sand or soil. Finally, both root and soil mycofloras were similar and both could be classed as 'acid' or 'alkaline' in type. These observations highlighted the importance of micro-environment and source of inoculum on the formation of a root surface community but still did not focus on crucial events in the succession on a particular substratum, i.e., hyphal colonization, interaction and replacement.

Scale and Pattern

As aptly phrased by Wiens (1989), our ability to detect pattern is a function of both the extent and the 'grain' of an ecological investigation. The scale at which fungal successions are observed must be varied both in time and space to reveal the pattern of individuals, patches and communities. It has been said of plants that, since almost all interactions in populations and communities are between neighbors, both empirical study and theoretical understanding must begin at this level (Harper, 1982). The same could be said of fungi, although neighbor has a broader meaning when referring to versatile, diffuse mycelia that may have extensive territories and cover considerable distances with cords or rhizomorphs.

The sampling techniques used by mycologists in successional studies have often been too ham-handed to preserve the microhabitats where hyphal interactions occur. All too often the substrata have been broken up and dispersed in a culture medium, so that patterns of individuals and species within populations and communities, familiar to higher-plant ecologists, were lost. There have been some notable exceptions.

Kendrick and Burges as early as 1962 gave us an excellent close-up view of species pattern in their description of fungi colonizing pine needles. One quotation alone indicates the intricate information to be found on a few square millimetres of a pine needle: "*Desmazierella* conidiophores, arising from the substomatal cavities, were unaffected by the distribution of *Helicoma* or *Sympodiella*, but were strongly influenced by the presence of *Lophodermium* diaphragms." More recently, intensive observations by Rayner and his co-workers of the 3-dimensional mosaic of individual mycelia, separated by interaction zones, in stumps and cut timber have altered our whole conception of fungal community development (Rayner, 1978; Rayner and Todd, 1979; Rayner and Boddy, 1988a, 1988b).

At higher levels of scale, the patchiness of microhabitats and clustering of species can be detected without disruption of the mycelia even when they are concealed in

litter or soil. For example, mapping and genetic analysis of the fruit bodies of agarics in quadrats of different sizes have revealed non-random, shifting patterns of mycelia (Swift, 1982b; Frankland, 1984). Extension and regression of mature mycelial systems in litter have also been examined by excavating and even reorientating them in the field (Thompson, 1984; Dowson et al., 1989).

At still higher levels of scale, features of fungal succession related to gross differences in habitat have been detected by using a wide variety of mathematical techniques, such as classification, ordination and regression, to analyze the data. For example, in a particularly intensive investigation, distribution patterns of soil microfungi in forest stands of northern Wisconsin were discerned by 3-dimensional ordination based on coefficients of similarity (Christensen, 1969). More recently, in an above-ground study, succession of basidiomycetous fruit bodies, in adjacent coniferous plantations of different ages, was inferred from regression models (Dighton, Poskitt and Howard, 1986). Thirdly, in the more defined conditions of grass roots in mine spoil under different treatments, the dynamics (including species turnover, composition, and abundance) of assemblages of saprotrophic species on roots over a 4-year period have also been described by mathematical functions (Zak, 1988; this volume). However, the risk of misinterpreting actual succession is bound to be high at this distance from one-to-one species interactions, particularly if the data are based on a mixture of active and inactive components or on fruiting, as was discovered in the well-known coprophilous example (Harper and Webster, 1964; see also, Suzuki, 1989). The influence of succession on community pattern and vice versa will only be resolved by a multi-scale approach.

MECHANISMS OF SUCCESSION

Evolutionary Adaptations

"The kernel of the idea of succession is obviously evolution" (Johnson, 1979). This fundamental premise is not always uppermost in mycologists' thoughts when mechanisms of succession are considered. Although the element of chance renders each succession unique, recognizable communities do develop as a result of underlying ecological adaptations interacting with the environment and specific substrata. Differential species performance is the core process (Pickett and McDonnell, 1989).

In attempts to unravel mechanisms, members of a succession can be helpfully categorized according to features that appear to be adaptive to early, mid- and late stages of succession. Among several categories of evolutionary selection or ecological 'strategy' suggested by ecologists (see Andrews, this volume), two or more have been recognized in fungal successions. As has been pointed out (Rayner and Boddy, 1988a; Pugh and Boddy, 1988), these strategies are flexible, changing with circumstances and stage of life-cycle, and are also relative, depending on which species are being compared.

Grime (1979) proposed three ecological strategies for plants which have been adopted by mycologists, namely R (ruderal), C (competitive) and S (stress). His scheme is related to the r-K concept as currently interpreted, although this originally referred to crowded and uncrowded situations (MacArthur and Wilson, 1967; Grubb, 1987). The R, C and S strategies encompass respectively species with short life spans and high reproductive capacity adapted to pioneer situations; those with well-developed competitive abilities, and more selective species adapted to a sustained existence under

stress conditions. Several variants on the same theme are recognizable in saprotrophic successions (Cooke and Rayner, 1984). Mucorales are typically ruderals, but frequently more than one strategy is exhibited within a single taxonomic group. Among Basidiomycotina, Rayner and Todd (1979) found, for example, that *Chondrostereum purpureum*, an early colonist of hardwood stumps, grew rapidly, fruited rapidly, and was quickly replaced, whereas later colonizers, such as *Hypholoma fasciculare*, were more competitive in terms of their ability to replace other species.

Ecological strategies are also apparent in successions of ectomycorrhizal species. Some of the most exciting successional studies of recent years have been on this group of fungi in temperate forests and plantations, particularly in association with *Betula*, *Picea* and *Pinus*. The ring and spur patterns of fruiting found around individual trees reflect successions on individual roots that can be likened in some respects to the substratum type of succession (Last, Mason, Wilson and Deacon, 1983; Last, Mason, Ingleby and Fleming, 1984; Mason et al., 1988; Fig.2), whereas the sequences of fruit bodies that occur at different stages of forest development can be described as seral (Dighton and Mason, 1985; Last, Dighton and Mason, 1987). In young forest stands of first generation trees, a narrow selection of ectomycorrhizal agarics with a broad host-range (R-selection), e.g. *Laccaria proxima*, was common (Fig. 3). The species in this

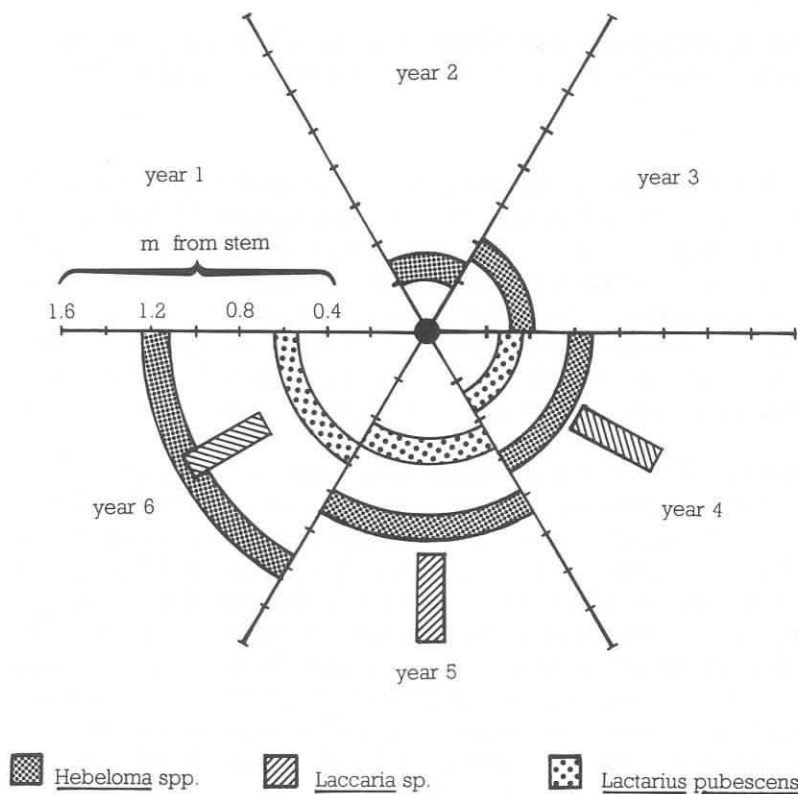


Figure 2 Succession of fruit bodies of ectomycorrhizal fungi around trees of *Betula*. The mean spatial distribution during the first six years after planting. (Redrawn from Last, Mason, Wilson and Deacon, 1983).

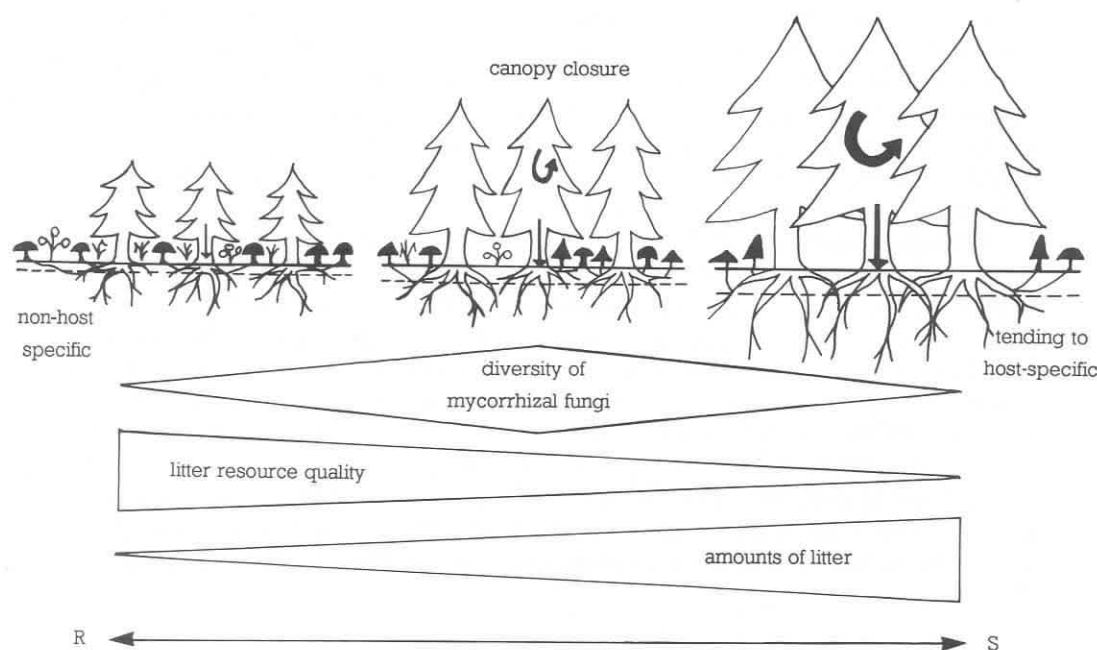


Figure 3 Diagram to illustrate succession of mycorrhizal fungi during forest development, associated with R- and S-selection and nature of the litter resource (after Dighton and Mason, 1985).

group tended to fruit prolifically, producing relatively small fruit bodies without cords, and they appeared to have a low demand for host carbohydrates. The diversity of mycorrhizal fungi increased up to closure of the tree canopy and then declined. Finally, when litter that was poor in nutrients had accumulated, late-comers to the succession, e.g. *Amanita muscaria*, typified an S-selection group. These species were more host-selective and altogether more persistent. They produced larger and fewer fruit bodies, often possessed cords and were possibly more demanding of energy derived from their hosts. In laboratory experiments, they required more glucose than some of the early-stage species.

The seral pattern of ectomycorrhizal succession in temperate forests appears to be repeated worldwide from the lowlands of Britain to the mountains of India (P.A. Mason, unpublished). Apparent anomalies have, however, been noticed. For example, after clear felling and replanting, early-stage fungi are usually bypassed. Similarly, if non-mycorrhizal seedling trees are planted among mature trees they are often colonized by species of the S-group including *Amanita*. Experimental manipulation of the succession has provided some explanations. In simple, axenic cultures, *Betula* could be 'infected' by both early- or late-stage fungi, so incompatibility between the host and different partners did not appear to be an important factor. Successful colonization did, however, depend partly on inoculum potential (p. 393) and soil type. In unsterile soil with added inocula, only early-stage fungi were ready colonizers (Deacon et al., 1983). This was borne out by trenching and coring experiments in the field, in which late-stage fungi when severed from their host food-base were poor colonizers of tree seedlings (Fleming, 1983, 1984; Fleming et al., 1986). These findings appear to be relevant to the

situation in second generation forests where at replanting, unlike conditions on a virgin site, impoverished litter has already accumulated. In addition, mature trees are often growing nearby, supporting late-stage fungi that are potential colonizers, adapted to stress conditions and able to outcompete the usual pioneers.

The mycorrhizal succession described illustrates how the recognition of ecological strategies can be more than just a theoretical exercise, since it could have major practical consequences in forestry. Choice of ectomycorrhizal fungi for use as inocula in the establishment of trees should, for example, take into account their likely competitive performance at different stages of forest development (Dighton and Mason, 1985).

A Causal Hierarchy

Although species with their inherent individualities play the central role in fungal succession, a hierarchy of causes controls its direction and outcome. A three-level classification of causes and mechanisms of succession in vegetation, proposed by Pickett et al. (1987), can also be applied to fungi, providing a useful framework for clarifying the whole complex of interactions.

At the highest level of the hierarchy are general causes of succession, such as the availability of space and availability of species of differential performance. The intermediate level contains all the processes and phenomena that condition the first, including dispersal, competition and grazing. Then at the most detailed level are the factors that define the outcome of the latter. These defining factors, for example, differential rates of growth and nutrient-uptake, operate between populations and individuals.

An investigation of a relatively simple but natural system, in which two decomposer basidiomycetes appeared to be competing for the same space and resources, illustrates how a hierarchy of causes might operate in succession (Newell, 1980, 1984a, 1984b; Frankland, 1984). Mixed clumps of the fruit bodies of *Mycena galopus* and *Marasmius androsaceus* were found to be common in a *Picea* plantation, but they originated from mycelia in two different zones of the needle litter. *Marasmius* occurred in the surface litter, whereas *Mycena* occupied the F1 horizon (unless it was growing separately, when it occupied the L layer), arriving according to the evidence as spores or by hyphal extension. Conversely, *Marasmius*, in the absence of *Mycena*, was capable of surviving in, and fruiting from, the F1 horizon. However, in laboratory experiments *Marasmius* always outcompeted *Mycena*; not only its growth rate but also its efficiency as a decomposer in terms of biomass was greater. The vertical juxtaposition of the mycelia of the two species was, therefore, somewhat of an enigma, until animal involvement was considered.

From field and laboratory experiments, the most abundant collembolan in the spruce litter, a species of *Onychiurus*, was found to graze *Marasmius androsaceus* more heavily than *Mycena galopus*, and to be subject to desiccation, retreating periodically from the surface litter to lower depths. It could be hypothesized, therefore, that selective grazing of *Marasmius* gave *Mycena* the advantage in the F1 horizon, but, at the surface, *Marasmius*, with its persistent rhizomorphs, escaped over-grazing when the litter dried out. The hypothesis is no doubt an over-simplification of the mechanisms and needs further testing. Nevertheless, evidence from several sources suggested that selective grazing and changes in the micro-environment were major factors controlling the availability of the species, and that differential rates of both growth and decomposer activity were among determinants of the final outcome of competition.

Arrival and Establishment

Succession can be conveniently considered as a 3-stage process of arrival, establishment and replacement, although this can belie its true complexity. Community development within succession, in its broad sense, has many pathways and many of them are not in themselves successional events. For example, mycoparasitism may occur, mycelia may become deadlocked with each other, or somatically compatible individuals may unite without replacement. Fig. 4 illustrates how broad and narrow views of events occurring during the colonization of a substratum can lead to misinterpretations of succession.

Early investigators focused on arrival by spores rather than mycelium. The ubiquity of fungal spores, discrete, readily quantified units, is notorious, so much so that the potential mycofloras of various soils are sometimes suggested to be the same. Certainly, arrival of spores on a particular substratum is usually considered to be a largely random process of selection, although the supply depends on such factors as: distance from a source; topography; season; life cycles; and dispersal mechanisms (controlled and passive). Relative rates of settling out from the air spora, or of emergence of germlings from extraneous deposits are also relevant, but adaptations for the firm attachment and adhesion of spores to the substratum appear, as expected, to be less significant in terrestrial than in aquatic environments.

The migration course of non-pathogen spores are rarely predictable, but Allen, Hippias and Wooldridge (1989) showed that spores of vesicular-arbuscular fungi could be dispersed by wind over considerable distances, alighting in predictable, non-random patterns dictated by wind dynamics and topography. The arrival time of spores on a virgin substratum is also not often known. Meredith (1959), however, obtained some evidence of when fungal spores landed on pine stumps, by recording fungal growth on

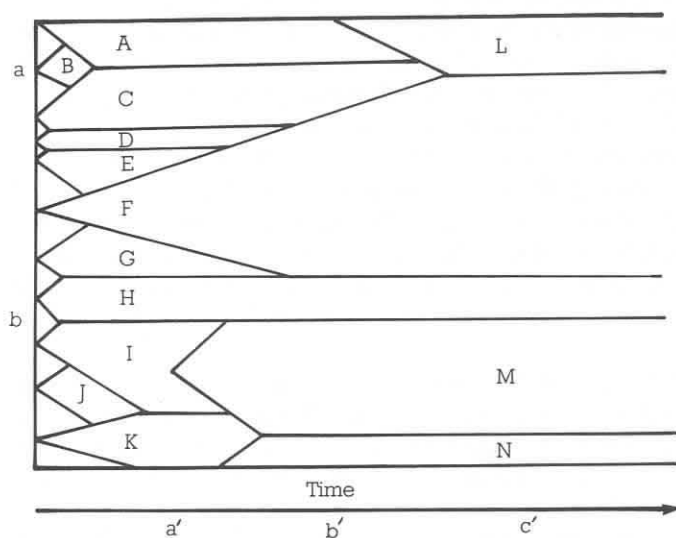


Figure 4 Diagram of fungal community development within a spatially-defined resource. The total colonizable space is represented by the gap between the top and bottom horizontal axes, and the fungal mycelia as A-N. Horizontal lines between adjacent bands indicate deadlock interactions; oblique ones indicate replacement. It illustrates the distorted interpretation of events that could occur by viewing them at points a and b, or in time from points a', b', and c'. (See Rayner and Todd, 1979, from which this is redrawn, for further details.)

incubated samples of the wood at hourly and daily intervals after felling. Small isolated colonies were assumed to have arisen from single spores. He was also able to deduce that the relative proportions of spores in the air above the stump influenced the incidence of infection by various species.

Arrival of mycelium on a substratum is a less passive process. Evidence that fungi possess attributes that enable them to explore and exploit resources efficiently continues to accumulate. Recognition responses, directional growth towards a resource, flexibility of growth-form, latent invasion, and the ability of the thallus to behave as a single, coordinated unit conserving biomass and energy have now been described in several species and situations (see Harley and Smith, 1983; Cooke and Rayner, 1984; Rayner, Boddy and Dowson, 1987a; Rayner, 1988).

The advantages for a saprotroph of establishment by mycelium have been summarized by Cooke and Rayner (1984) as: rapid and effective resource capture, synergism between individual hyphae, and reduction in problems associated with somatic incompatibility which are a feature of genetically different spores. Continuous substrata, such as a forest litter layer or soil, with which direct contact can be made, are most suited to this type of invasion. Proximity is a fundamental requisite. The succession of fungi on decaying wood on a forest floor has been found, for example, to vary according to whether it is exposed to species in the air, litter or other rotting wood (Carruthers and Rayner 1979).

In a pioneer situation, competition may not be met by a spore or mycelium immediately, and nearness of neighbors may even be beneficial. Both stimulation and inhibition of germination are well known to occur in spore deposits. In addition, somatic compatibility of adjacent colonies can lead to the formation of larger units ousting smaller individuals. Many other factors such as shortage of nutrients and grazing may influence survival and establishment at this stage before true competition (i.e. hardships from nearness of neighbors) begins. It is therefore not surprising that it is characterized by ruderal species unadapted for 'combat'.

As a fungal community closes in, hardships from nearness of neighbors and overlap of niches are likely to increase, and there may be competition for limited resources. The success of a fungus in establishing itself on a substratum against such competition depends on many interactions. The intrinsic factors of a saprotroph that contribute to this success were summed up by Garrett (1950, 1956, 1970) in two terms, originally proposed for root-infecting fungi: competitive saprophytic ability and inoculum potential. The first is "the summation of physiological characteristics that make for success in competitive colonization of dead organic substrates" (1956; p. 130). It includes such attributes as rapid rates of growth and germination, and the ability to produce specific enzymes and antibiotics. It is not a fixed character but substratum specific, its expression depending on the immediate conditions. In plant ecology it is matched by the term "competitive ability" or "competitive capacity". Mueller-Dombois and Ellenberg (1974, p. 352), writing of higher-plant communities, stated that, in general, "the competitive ability of a species depends on its genetic potential which is manifested in its morphological structure and physiological requirements" and "varies with habitat factors, it is not a constant species property" (p. 353).

The inoculum potential of a saprotrophic fungus was defined by Garrett (1956, p. 41) as "the energy of growth of a fungus available for colonization of a substrate at the surface of the substrate to be colonized". It is governed by such factors as propagule density, hyphal age, and (*sensu* Garrett) conditions in the environment, including, for example, grazing pressure and diffusion of nutrients from the substratum. Success will

depend partly on the balance between the competitive saprotrophic ability and the inoculum potential. A poor competitive saprotroph might gain advantage by having a relatively high inoculum potential. Plant ecologists do not appear to have a general term for this invasive force of a colonist, but examples of the combined effect of the competitive ability of a plant and its age, performance, or population level on community patterns are frequently quoted.

Garrett's concepts apply particularly, in Cooke and Rayner's (1984) terminology, to primary resource capture, but when contact between mycelia occurs more combative attributes are required if distinct territories are to be delimited. Antagonistic reactions, such as the production of pigmented zones, mycelial barrages and lysis, so characteristic of Basidiomycotina, mark this stage. The result can be deadlock (neither mycelium advancing into the other) or finally, as the competitive balance changes, replacement of one by the other.

Replacement

The crux of succession is replacement of individuals. Evidence that an association of fungi, any more than a plant community, behaves as a unit in terms of succession is negligible. As Miles (1987) said of vegetation: to act in this way, "it would need to be a tightly integrated network of species, probably co-evolved and co-adapted. . . ."

As already discussed, a hierarchy of causes is involved in succession, and actual replacement occurs when one individual acquires a decisive advantage over another. Higher-plant ecologists have attempted to explain this with models such as Horn's (1981) obligatory succession model and Connell and Slatyer's (1977) facilitation model; in both of these earlier species 'pave the way' for later species and facilitate replacement. Alternative mechanisms of replacement in higher-plant succession were described by Connell and Slatyer's tolerance and inhibition models. In the tolerance situation, late colonists replace early species because they can grow better at lower levels of resources; they are successful whether or not earlier species have preceded them. In the inhibition model, early occupants of the site are considered to modify the micro-environment so that it becomes less suitable for subsequent colonization by both early and late species, and the early species are killed not by competition as in the other models but by some local disturbance such as grazing or frost. Any of the three mechanisms of facilitation, tolerance and inhibition could operate in a fungal decomposer succession, but they are unlikely to act singly or to be associated only with particular species.

Modification of the site is inevitable following occupation. On a substratum such as the bracken litter already described, a species might improve it for a successor or impair it for itself by, for example, accumulation of nitrogen, exhaustion of pectin, removal of tannins, or changes in physical structure. *Trichoderma* did not become prominent until the second year of the succession, when it parasitized live mycelium of *Mortierella*, grew over moribund mycelium of its predecessors, and also penetrated deeply into xylem vessels and fibers. The decomposition rate of sterilized bracken by this species was doubled by addition of nitrogen, so its field performance may have depended partly on a supply of fungal nitrogen, but one can only speculate from in vitro experiments. The production of sugars as by-products of cellulose decomposition is another often-quoted example of the possible priming of a substratum, and already mentioned in relation to bracken decomposition. In the same succession, *Mycena galopus* might also appear to depend on changes brought about by earlier colonists, but in monoculture it grew equally well on recently fallen and old, weathered litter (Frankland, 1981).

There is little evidence that a species dies out in fungal successions from starvation or senility. Accumulation of nutrients may often be more important than exhaustion of supply. Garrett's generalized hypothesis (1963) of a nutritional sequence on plant debris of 'sugar fungi' followed by cellulose and lignin decomposers was widely accepted until exceptions were noted (see Swift, 1976). The relationship between substratum composition and fungal function is far from clear cut, many species having wide enzymic capabilities. Nor is the survival time of a decomposer necessarily related to its performance. *Hypoxylon multifforme*, for example, is capable of only moderate decay of hardwood but can persist for long periods in dead stumps among competitors, whereas *Coriolus versicolor*, capable of the complete breakdown of woody tissue, is often replaced by more competitive fungi at a relatively early stage (Rayner and Todd, 1979).

Many examples of the production and removal of inhibitors that might influence replacement could be quoted. When fungi from *Quercus* leaf litter were tested for inhibition by tannins, some early colonists were tolerant, whereas later species that grew when the concentration of tannins in the litter would be lower were inhibited (Harrison, 1971). It is tempting to 'explain' succession in this way, but several other species did not fit the hypothesis, emphasizing again the need for a multivariate approach.

The effects on replacement of changes in the physical character of a substratum, such as particle size, are probably overlooked more often than the chemical aspects. The initial breakdown of a plant organ by pioneer fungi is likely to increase aeration of the internal tissues and access for the less diffusible fungal enzymes. *Mycena galopus* entered bracken petioles when there were breaks in the epidermis and tunnels in the interior; it then formed, around its hyphae, characteristic 'bore-hole' cavities in the fiber walls. It appeared to be equipped to decompose chunks of hard plant tissue, unlike other members of the succession with more diffusible enzymes. Nilsson (1974, 1976) suggested that the cellulase production of some wood-attacking microfungi is stimulated by the physical structure of a substratum and that, in some cases, enzymes are produced only when a hypha in a plant cell wall is growing parallel to the cellulose microfibrils.

The actual process by which an individual mycelium yields space, like the cause, varies with the species combination. Although the sampling techniques used in many past studies of succession destroyed the evidence, several replacement processes have now been observed. Most of these have been between paired fungi, particularly Basidiomycotina, on culture media or natural substrata in the laboratory, and in samples of wood and non-sterile soil or litter in the field (e.g., Rypáček, 1966; Rayner and Todd, 1979; Rayner et al., 1987a; Dowson et al., 1988a, 1988b). Evidence of past replacements is also frequently to be seen in the field, particularly in stumps and logs where fungal decomposers have been active, for example: relict zone lines within another interaction area; a series of zone lines in front of an advancing mycelium; or a species growing only at the periphery of a decay column occupied by a second species. In general, the interactions observed in the laboratory and field between the same species have corresponded closely, indicating the importance of inherent combative abilities. In addition, evolutionary trends are also suggested, i.e. species present at the later stages of a succession are more competitive than earlier colonists in terms of their ability to replace others, even within a single taxonomic group (Rayner and Todd, 1979).

Initially, one fungus may colonize literally on top of another, or, if two adjacent mycelia are interacting at their margins, when one is inhibited the other may grow over or through its neighbor, eventually replacing all or part of it. The process can vary greatly in speed and can be described as passive, or active if it involves parasitism or

some type of antagonism, such as 'hyphal interference' in which death follows contact without fusion (Ikediugwu and Webster, 1970, Traquair and McKeen, 1977). Usually the 'aggressor' slows before it overgrows the partner, sometimes lysing it, but some species are replaced much more rapidly and appear to be parasitized, e.g., *Bjerkandera adusta* by *Pseudotrametes gibbosa* (Rayner and Boddy, 1988a). Mycoparasitism may involve necrotrophy in which nutrients in the hyphae are utilized after death, but the evidence for this often is sparse. An unusual strategy is that of temporary parasitism in which the parasite appears to gain a large mycelial domain rather than a food source, allowing it to produce large reproductive structures. This has been described in the replacement of pioneer *Coriolus* spp. by *Lenzites betulina* in wood (Rayner, Boddy and Dowson, 1987b).

The molecular mechanisms underlying the various replacement phenomena are obscure. The involvement of genetic regulatory processes and signalling systems has been suggested, since developmental shifts commonly accompany the interactions (Rayner and Boddy, 1988a). Exciting possibilities for probing the links between fungal development and ecology have been indicated in a discussion of some cultural studies of the forest pathogen *Heterobasidion annosum* (Stenlid and Rayner, 1989).

THE FUTURE

Increasing integration of description, theory and experiment has marked successional studies of fungi in the last decade. Alongside broad ecosystem analyses of more general ecology, the underlying processes and individual responses of fungi are now being examined rather than endpoints. The approach is often reminiscent of the early reductionist views of Gleason (1926), who stressed the importance in plant succession of individual properties.

At the descriptive stage, patterns of mycelia on many substrata in the field are still largely unexplored. Many more comparative studies are also required before generalizations can be made. The number of species combinations so far examined is relatively very small. Nevertheless, some ecological abstraction, by subjective selection of the key species in a system, seems likely to be the best way forward, the choice depending on both abundance and competitive dominance. Hypotheses for testing can then be formulated. As said by Keddy (1989): "Data are important for falsifying hypotheses, but bold conjecture or original hypotheses are what drive scientific progress".

The problems of over-simplification in microcosms and of interpretation when natural successions are manipulated are well-known. The 'fundamental' niche of a species as determined in the laboratory is likely to be much broader than the 'realized' niche of an individual exposed to the competition of the complete biota. Successions in the field have been inhibited or accelerated by, for example, trenching to cut off mycorrhizal hosts, or addition of nutrients and biocides. Spectacular changes and clues are obtained in this way, but the systems are still complex.

More experiments that bridge the gap between laboratory and field need to be devised for the testing of hypotheses. Garrett (1970) and his co-workers' classic experiments, in which they recorded the competitive colonization of 'units' of straw, buried in soil containing fungi at various inoculum levels, were fore-runners of this approach. More recently, various aspects of succession have been explored successfully, using such techniques as burial of inoculated substrata in the field, soil recolonization tubes, and 'trap' plants for mycorrhizal fungi. These and other relevant methods have been reviewed by Frankland et al. (1990).

The progress made in understanding the modes and mechanisms of fungal succession by focusing on the mycelium has been emphasized in this chapter. Continued research at this level of investigation and below, while mathematicians cope with the multivariate aspects, should lead eventually to greater precision in predicting outcomes, with many practical applications. Fresh impetus may also come by drawing back from the scene and providing data for the modeler. As Usher (1987) acknowledged, the greatest role of models is probably in clarifying the concepts included in them, and in generating feedbacks between them and further investigations. However, to reiterate—as “succession is the natural integration of all ecosystem processes”, it will remain “among the most complex and difficult to unravel of ecological phenomena” (McNaughton and Wolf, 1973).

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REFERENCES

- Allen, M. F., Hipps, L. E., and Wooldridge, G. L. (1989). Wind dispersal and subsequent establishment of VA mycorrhizal fungi across a successional arid landscape. *Landsc. Ecol.* 2: 165–171.
- Brown, J. C. (1958a). Soil fungi of some British sand dunes in relation to soil type and succession. *J. Ecol.* 46: 641–664.
- Brown, J. C. (1958b). Fungal mycelium in dune soils estimated by a modified impression slide technique. *Trans. Brit. Mycol. Soc.* 41: 81–88.
- Carruthers, S. M., and Rayner, A. D. M. (1979). Fungal communities in decaying hardwood branches. *Trans. Brit. Mycol. Soc.* 72: 283–289.
- Christensen, M. (1969). Soil microfungi of dry to mesic conifer-hardwood forests in northern Wisconsin. *Ecology* 50: 9–27.
- Clements, F. E. (1916). Plant succession. An analysis of the development of vegetation. *Carnegie Inst. Wash. Publ. No. 242*.
- Connell, J. H., and Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Natur.* 111: 1119–1144.
- Cooke, R. C., and Rayner, A. D. M. (1984). *Ecology of Saprotrophic Fungi*. Longman, New York.
- Deacon, J. W., Donaldson, S. J., and Last, F. T. (1983). Sequences and interactions of mycorrhizal fungi on birch. *Pl. Soil* 71: 257–262.
- Dickinson, C. H., and Pugh, G. J. F. (Eds.). (1974). *Biology of Plant Litter Decomposition*. Academic Press, New York.
- Dighton, J., and Mason, P. A. (1985). Mycorrhizal dynamics during forest tree development. In *Developmental Biology of Higher Fungi*, D. Moore, L. A. Casselton, D. A. Wood and J. C. Frankland (Eds.). Cambridge University Press, New York, pp. 117–139.
- Dighton, J., Poskitt, J. M., and Howard, D. M. (1986). Changes in occurrence of basidiomycete fruit bodies during forest stand development: with specific reference to mycorrhizal species. *Trans. Brit. Mycol. Soc.* 87: 163–171.
- Dowson, C. G., Rayner, A. D. M., and Boddy, L. (1988a). Inoculation of mycelial cord-forming basidiomycetes into woodland soil and litter. II. Resource capture and persistence. *New Phytol.* 109: 343–349.
- Dowson, C. G., Rayner, A. D. M., and Boddy, L. (1988b). The form and outcome of mycelial interactions involving cord-forming decomposer basidiomycetes in homogeneous and heterogeneous environments. *New Phytol.* 109: 423–432.

- Dowson, C. G., Rayner, A. D. M., and Boddy, L. (1989). Spatial dynamics and interactions of the woodland fairy ring fungus, *Clitocybe nebularis*. *New Phytol.* 111: 699–705.
- Fleming, L. V. (1983). Succession of mycorrhizal fungi on birch: infection of seedlings planted around mature trees. *Pl. Soil* 71: 263–267.
- Fleming, L. V. (1984). Effects of soil trenching and coring on the formation of ectomycorrhizas on birch seedlings grown around mature trees. *New Phytol.* 98: 143–153.
- Fleming, L. V., Deacon, J. W., and Last, F. T. (1986). Ectomycorrhizal succession in a Scottish birch wood. In *Physiological and Genetical Aspects of Mycorrhizae*, V. Gianinazzi-Pearson and S. Gianinazzi (Eds.). Institut National de la Recherche Agronomique, Paris, pp. 259–264.
- Frankland, J. C. (1966). Succession of fungi on decaying petioles of *Pteridium aquilinum*. *J. Ecol.* 54: 41–63.
- Frankland, J. C. (1969). Fungal decomposition of bracken petioles. *J. Ecol.* 57: 25–36.
- Frankland, J. C. (1976). Decomposition of bracken litter. *Bot. J. Linn. Soc.* 73: 133–143.
- Frankland, J. C. (1981). Mechanisms in fungal successions. In *The Fungal Community. Its Organization and Role in the Ecosystem*, D. T. Wicklow and G. C. Carroll (Eds.). Marcel Dekker, New York, pp. 403–426.
- Frankland, J. C. (1984). Autecology and the mycelium of a woodland litter decomposer. In *The Ecology and Physiology of the Fungal Mycelium*, D. H. Jennings and A. D. M. Rayner (Eds.). Cambridge University Press, New York, pp. 242–260.
- Frankland, J. C. (1989). Fungal succession: myth or reality? In *Recent Advances in Microbial Ecology*, T. Hattori et al., (Eds.). Proc. 5th Int. Symp. Microbial Ecology, Kyoto, 1989, Japan Scientific Societies Press, Tokyo, pp. 255–259.
- Frankland, J. C., Dighton, J., and Boddy, L. (1990). Methods for studying fungi in soil and forest litter. In *Methods in Microbiology*, Vol 22, R. Grigorova and J. R. Norris (Eds.) Academic Press, New York, pp 343–404.
- Garrett, S. D. (1950). Ecology of the root-infecting fungi. *Biol. Rev.* 25: 220–254.
- Garrett, S. D. (1956). *Biology of Root-Infecting Fungi*. Cambridge University Press, New York.
- Garrett, S. D. (1963). *Soil Fungi and Soil Fertility*. Pergamon Press, New York.
- Garrett, S. D. (1970). *Pathogenic Root-infecting Fungi*. Cambridge University Press, New York.
- Gleason, H. A. (1926). The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7–26.
- Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. John Wiley, New York.
- Grubb, P. J. (1987). Some generalizing ideas about colonization and succession in green plants and fungi. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.). Blackwell Sci. Publ., Oxford, England, pp. 81–102.
- Harley, J. L., and Smith, S. E. (1983). *Mycorrhizal Symbiosis*. Academic Press, New York.
- Harper, J. E., and Webster, J. (1964). An experimental analysis of the coprophilous fungus succession. *Trans. Brit. Mycol. Soc.* 47: 511–530.
- Harper, J. L. (1982). After description. In *The Plant Community as a Working Mechanism*, E. I. Newman (Ed.). Blackwell Sci. Publ., Oxford, England, pp. 11–25.
- Harrison, A. F. (1971). The inhibitory effect of oak leaf litter tannins on the growth of fungi in relation to litter decomposition. *Soil Biol. Biochem.* 3: 167–172.
- Horn, H. S. (1974). The ecology of secondary succession. *Ann. Rev. Ecol. Syst.* 5: 25–37.
- Horn, H. S. (1981). Succession. In *Theoretical Ecology. Principles and Applications*, R. M. May (Ed.). Blackwell Sci. Publ., Oxford, England, pp. 253–271.
- Hudson, H. J. (1968). The ecology of fungi on plant remains above the soil. *New Phytol.* 67: 837–874.
- Ikediugwu, F. E. O., and Webster, J. (1970). Hyphal interference in a range of coprophilous fungi. *Trans Brit. Mycol. Soc.* 54: 205–210.
- Johnson, E. A. (1979). Succession: an unfinished revolution. *Ecology* 60:238–240.
- Keddy, P. A. (1989). *Competition*. Chapman and Hall, New York.
- Kendrick, W. B., and Burges, A. (1962). Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia* 4:313–342.

- Last, F. T., Mason, P. A., Wilson, J., and Deacon, J. W. (1983). Fine roots and sheathing mycorrhizas: their formation, function and dynamics. *Pl. Soil* 71: 9–21.
- Last, F. T., Mason, P. A., Ingleby, K., and Fleming, L. V. (1984). Succession of fruitbodies of sheathing mycorrhizal fungi associated with *Betula pendula*. *For. Ecol. Manage.* 9: 229–234.
- Last, F. T., Dighton, J., and Mason, P. A. (1987). Successions of sheathing mycorrhizal fungi. *Trends Ecol. Evol.* 2: 157–161.
- Levin, S. A. (1989). Challenges in the development of a theory of community and ecosystem structure and function. In *Perspectives in Ecological Theory*, J. Roughgarden, R. M. May and S. A. Levin (Eds.). Princeton University Press, Princeton, New Jersey, pp. 242–255.
- MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography*, Princeton University Press, Princeton, New Jersey.
- Mason, P. A., Last, F. T., Wilson, J., Deacon, J. W., Fleming, L. V., and Fox, F. M. (1988). Fruiting and succession of ectomycorrhizal fungi. In *Fungal Infection of Plants*, G. F. Pegg and P. G. Ayres (Eds.). Cambridge University Press, New York, pp. 253–268.
- McNaughton, S. J., and Wolf, L. L. (1973). *General Ecology*. Holt, Rinehart and Winston, New York.
- Meredith, D. S. (1959). The infection of pine stumps by *Fomes annosus* and other fungi. *Ann. Bot. (London) [N. S.]* 23: 455–476.
- Miles, J. (1979). *Vegetation Dynamics*. Chapman and Hall, New York.
- Miles, J. (1987). Vegetation succession: past and present perceptions. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley, and P. J. Edwards (Eds.). Blackwell Sci. Publ., Oxford, England, pp. 1–29.
- Mueller-Dombois, D., and Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. Wiley, New York.
- Newell, K. (1980). *The Effect of Grazing by Litter Arthropods on the Fungal Colonization of Leaf Litter*. Ph. D. Thesis, University of Lancaster, England.
- Newell, K. (1984a). Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. *Soil Biol. Biochem.* 16: 227–233.
- Newell, K. (1984b). Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. *Soil Biol. Biochem.* 16: 235–239.
- Nilsson, T. (1974). Microscopic studies on the degradation of cellophane and various cellulosic fibres by wood-attacking microfungi. *Studia Forestalia Suecica No. 117*.
- Nilsson, T. (1976). Soft-rot fungi-decay patterns and enzyme production. In *Organismen und Holz*, G. Becker and W. Liese (Eds.). Internationales Symposium, Berlin-Dahlem, 1975. Duncker and Humblot, Berlin, pp. 103–112.
- Park, D. (1968). The ecology of terrestrial fungi. In *The Fungi*, Vol. 3, G. C. Ainsworth and A. S. Sussman (Eds.). Academic Press, New York, pp. 5–39.
- Peet, R. K., and Christensen, N. L. (1980). Succession: a population process. *Vegetatio* 43: 131–140.
- Pickett, S. T. A., Collins, S. L., and Armesto, J. J. (1987). A hierarchical consideration of causes and mechanisms of succession. *Vegetatio* 69: 109–114.
- Pickett, S. T. A., and McDonnell, M. J. (1989). Changing perspectives in community dynamics: a theory of successional forces. *Trends Ecol. Evol.* 4: 241–245.
- Pugh, G. J. F., and Boddy, L. (1988). A view of disturbance and life strategies in fungi. In *Fungi and Ecological Disturbance*, L. Boddy, R. Watling and A. J. E. Lyon (Eds.). *Proc. Roy. Soc. Edinb.* 94B: 3–11.
- Rayner, A. D. M. (1978). Interactions between fungi colonizing hardwood stumps and their possible role in determining patterns of colonization and succession. *Ann. Appl. Biol.* 89: 131–134.
- Rayner, A. (1988). Life in a collective: lessons from the fungi. *New Scientist* No. 1639: 49–53.
- Rayner, A. D. M., and Todd, N. K. (1979). Population and community structure and dynamics of fungi in decaying wood. *Adv. Bot. Res.* 7: 333–420.

- Rayner, A. D. M., Watling, R., and Frankland, J. C. (1985). Resource relations—an overview. In *Developmental Biology of Higher Fungi*, D. Moore, L. A. Casselton, D. A. Wood and J. C. Frankland (Eds.). Cambridge University Press, New York, pp. 1–40.
- Rayner, A. D. M., Boddy, L., and Dowson, C. G. (1987a). Genetic interactions and developmental versatility during establishment of decomposer basidiomycetes in wood and tree litter. In *Ecology of Microbial Communities*, M. Fletcher, T. R. G. Gray and J. G. Jones (Eds.). Cambridge University Press, New York, pp. 83–123.
- Rayner, A. D. M., Boddy, L. and Dowson, C. G. (1987b). Temporary parasitism of *Coriolus* spp. by *Lenzites betulina*: a strategy for domain capture in wood decay fungi. *FEMS Microbiol. Ecol.* 45: 53–58.
- Rayner, A. D. M., and Boddy, L. (1988a). *Fungal Decomposition of Wood: its Biology and Ecology*. John Wiley, New York.
- Rayner, A. D. M., and Boddy, L. (1988b). Fungal communities in the decay of wood. *Adv. Microb. Ecol.* 10: 115–136.
- Rypáček, V. (1966). *Biologie holzzerstrender Pilze*. Fischer, Jena.
- Stenlid, J., and Rayner, A. D. M. (1989). Tansley Review No. 19. Environmental and endogenous controls of developmental pathways: variation and its significance in the forest pathogen, *Heterobasidion annosum*. *New Phytol.* 113: 245–258.
- Suzuki, A. (1989). Analyses of factors affecting the occurrence and succession of the ammonia fungi. In *Recent Advances in Microbial Ecology*, T. Hattori et al. (Eds.). Proc. 5th Int. Symp. Microbial Ecology, Kyoto, 1989. Japan Scientific Societies Press, Tokyo, pp. 275–279.
- Swift, M. J. (1976). Species diversity and the structure of microbial communities in terrestrial habitats. In *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, J. M. Anderson and A. Macfadyen (Eds.). Blackwell Sci. Publ., Oxford, England, pp. 185–222.
- Swift, M. J. (1982a). Microbial succession during the decomposition of organic matter. In *Experimental Microbial Ecology*, R. G. Burns and J. M. Slater (Eds.). Blackwell Sci. Publ., Oxford, England, pp. 164–177.
- Swift, M. J. (1982b). Basidiomycetes as components of forest ecosystems. In *Decomposer Basidiomycetes: their Biology and Ecology*, J. C. Frankland, J. N. Hedger and M. J. Swift (Eds.). Cambridge University Press, New York, pp. 307–337.
- Swift, M. J. (1984). Microbial diversity and decomposer niches. In *Current Perspectives in Microbial Ecology*, M. J. King and C. A. Reddy (Eds.). Amer. Soc. Microbiol., Washington, pp. 8–16.
- Thompson, W. (1984). Distribution, development and functioning of mycelial cord systems of decomposer basidiomycetes of the deciduous woodland floor. In *The Ecology and Physiology of the Fungal Mycelium*, D. H. Jennings and A. D. M. Rayner (Eds.). Cambridge University Press, New York, pp. 185–260.
- Traquair, J. A., and McKeen, W. E. (1977). Hyphal interference in *Trametes hispida*. *Can. J. Microbiol.* 23: 1675–1682.
- Tribe, H. T. (1957). Ecology of micro-organisms in soils as observed during their development upon buried cellulose film. In *Microbial Ecology*, R. E. O. Williams and C. C. Spicer (Eds.). Cambridge University Press, New York, pp. 287–298.
- Tribe, H. T. (1961). Microbiology of cellulose decomposition in soil. *Soil Sci.* 92: 61–77.
- Usher, M. B. (1987). Modelling successional processes in ecosystems. In *Colonization, Succession and Stability*, A. J. Gray, M. J. Crawley and P. J. Edwards (Eds.). Blackwell Sci. Publ., Oxford, England, pp. 31–55.
- Visser, S. (1985). Role of the soil invertebrates in determining the composition of soil microbial communities. In *Ecological Interactions in Soil, Plants, Microbes and Animals*, A. H. Fitter (Ed.). Blackwell Sci. Publ., Oxford, England, pp. 297–317.
- Wicklow, D. T. (1988). Parallels in the development of post-fire fungal and herbal communities. In *Fungi and Ecological Disturbance*, L. Boddy, R. Watling and A. J. E. Lyon (Eds.). *Proc. Roy. Soc. Edinb.* 94B: 87–95.

Wiens, J. A. (1989). Spatial scaling in ecology. *Funct. Ecol.* 3: 385–397.

Zak, J. C. (1988). Redevelopment of biological activity in strip-mine spoils: saprotrophic fungal assemblages of grass roots. In *Fungi and Ecological Disturbance*, L. Boddy, R. Watling, and A. J. E. Lyon (Eds.). *Proc. Roy. Soc. Edinb.* 94B: 73–83.